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Small-scale Collembola community composition in a pine forest soil – Overdispersion in functional traits indicates the importance of species interactions

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ABSTRACT

Soil communities are considered to be remarkably species-rich and to have many generalist species with seemingly similar niche requirements. The composition of soil fauna communities is often highly variable even at the plot scale, and both the environment and the spatial configuration of microhabitats are regarded as important forces shaping the structure of local communities. However, to what extent these forces are important in different ecosystems is not clear. We examined the relative roles of environmental (abiotic), vegetation (biotic) and spatial variables (using Moran's eigenvector maps, MEM) for the small-scale variation in springtail (Collembola) communities in a 100 m^2 area of the forest floor of a mature Scots pine forest in central Sweden, with small variation in important environmental variables.

We found that most of the small-scale variation in community composition could be explained by spatial variables, either alone or jointly with the environmental variables. Spatial variability in community composition, in turn, could be related to shifts in functional traits of the component species. Within local communities (samples), species showed a higher diversity than expected by chance in almost all examined traits, indicating that differences in resource and micro-habitat utilisation enable Collembola species to coexist. Competition between species is therefore likely to be important for structuring Collembola communities at this spatial scale. The results indicate that the spatial scale of study and heterogeneity of environmental factors influence soil fauna community assembly processes through effects on the relative importance of environmental filtering compared to filtering by limiting similarity or competitive exclusion.

1. Introduction

Soil ecosystems are species-rich but what causes this high diversity of soil communities is less well known than for many aboveground living animals (Wardle, 2006). It has been argued that soil-dwelling species possess low niche specialisation, which is otherwise mostly found in less species-rich ecosystems (Anderson, 1975; Maraun et al., 2003; Digel et al., 2014). This assumed low niche segregation contradicts the theory on limiting similarity or competitive exclusion in community assembly (Hutchinson, 1959; MacArthur and Levins, 1967; HilleRisLambers et al., 2012; Violle et al., 2012) and begs the question: what is explaining this enigma of high soil fauna diversity (Anderson, 1975; Giller, 1996)? There are different views on how such high local species richness is established and maintained. It has been explained by the three dimensional nature of soils with strong short-scale resource and habitat gradients allowing a high level of niche partitioning (Takeda, 1987; Berg and Bengtsson, 2007) or by coexisting species actually having a larger difference in feeding preference than previously known (Jorgensen et al., 2003; Schneider et al., 2004). Identifying the mechanisms that determine the variation in community composition of soil fauna is essential to understand the functioning of soil ecosystems and to better predict changes in communities from changes in land use or climate (Bardgett et al., 2005a).

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Soil fauna composition shows a large variation at the microscale (<1 m), where soil-pore-size distribution, soil microclimate, root structure and above-ground vegetation structure result in small-scale patchy distribution in environmental conditions that can affect local community composition (Berg and Bengtsson, 2007; Berg, 2012; Viketoft, 2013). Soil organisms often also show aggregated patterns of abundance at the mesoscale (a few meters up to 100 m) (Saetre, 1999; Ettema et al., 2000; Jimenez et al., 2006; Widenfalk et al., 2015). At these spatial scales environmental conditions, such as gradients in soil pH, soil moisture and vegetation composition, have appeared to have a large impact on soil organism distributions (Ettema and Wardle, 2002; Berg, 2012). The environmentally correlated variation in local community composition is often attributed to niche differences between species in, e.g., the tolerance to abiotic conditions such as soil pH and soil moisture. However, species interactions, e.g., competition and predation, and differences in home range and in dispersal limitation may also affect local community composition at small spatial scales (Gonzalez, 2009; Martins da Silva et al., 2012). For instance, the study by Martins da Silva et al. (2012) showed that Collembola in patches of fragmented forests had a higher dispersal ability compared to species that lived in the surrounding agricultural matrix. These studies suggest that local environmental conditions and spatial factors together drive community composition, but we know little of the relative importance of these factors.

One approach to understand spatiotemporal variation in community composition is to assess the role of different environmental and spatial factors simultaneously. This is possible by variation partitioning methods (Borcard et al., 1992) that examine how predictive variables (environmental or spatial factors) explain variation in community composition. The explained variation is divided between what is accounted for by either the pure spatial or the pure environmental fractions, and the shared (joint) contribution of both fractions. A significant environmental component indicates that differences in local habitat conditions drive variation in community composition, while a large contribution of the spatial component is interpreted as an indication that either small-scale dispersal limitation or biotic interactions and priority effects are important structuring forces (Cottenie, 2005).

An alternative approach to examining the mechanisms shaping community composition has been to examine what properties the coexisting species on a small scale possess compared to the total set of species observed, living in different microhabitats under various environmental conditions. This can be measured using information about species functional traits (hereafter termed “traits”) (McGill et al., 2006), as traits indicate the fit of species to a given environment (Violle et al., 2007). Communities with species that are more similar in traits than expected if species had been assembled randomly from a larger species pool, are called underdispersed or convergent. They are assumed to be influenced by strong environmental filtering that only allows species with a particular subset of traits to successfully establish (Cornwell et al., 2006). On the other hand, communities of species with traits that are less similar to each other than expected from a random assembly of species show overdispersion or divergence in traits. This is usually interpreted as structuring of the community by biotic interactions, especially competition, which exclude too similar species to coexist (Belyea and Lancaster, 1999; HilleRisLambers et al., 2012). Significant overdispersion suggests that a large part of the community variation explained by the spatial component is due to interactions that limit niche similarity between species, rather than dispersal limitation. Often both processes are operating at the same time, with environmental filtering being most important at larger scales (external filtering) while biotic interactions shape the communities at smaller scales (internal filtering) (Violle et al., 2012). Hence, the joint use of the two approaches can provide a more detailed information on the processes of community assembly.

Springtails (Collembola) are one of the ecologically and taxonomically best known soil animal taxa, and one of the most widespread and numerous soil arthropod groups (Petersen and Luxton, 1982; Bardgett et al., 2005b). Small-scale variation in community composition of springtails was mainly explained by environmental rather than spatial variables in a salt marsh affected by frequent flooding (Widenfalk et al., 2015). Russell and Griegel (2006) found that an initially strong effect of environmental variables after an inundation event decreased with time. Hence, the degree of environmental filtering of local communities as a structuring force may vary with, e.g., disturbance intensity and frequency. On the other hand, Collembola have also been shown to be sensitive towards increases in patch fragmentation and isolation, suggesting that spatial components may play a role in explaining community composition (Martins da Silva et al., 2012). The often strong responses of Collembola species to environmental and spatial factors make this group of soil fauna well suited to assess what is determining small-scale differences in species composition.

The aim of this study was to understand the impact of spatial factors and biotic interactions among Collembola. To this aim, we wanted variation in environmental factors to be relatively small. Hence we chose to study a habitat with a rather low environmental and vegetation composition heterogeneity. We explicitly focus on the horizontal spatial variation in community composition of Collembola, because vertically soil layers are not distinct separate habitats and many springtails commonly move between layers in response to weather and seasonal conditions (Krab et al., 2010, 2013). Furthermore, there is no simple measure that can translate between horizontal and vertical variation in an ecologically meaningful and consistent way in the soil. However, vertical variation in community composition between soil layers can be substantial (Ponge, 1993; Berg and Bengtsson, 2007). For this reason, we also examine whether vertical stratification in community composition can influence the interpretation of the results in a separate analysis (Tables S7 and S8). We examined the importance of spatial, environmental (abiotic) and vegetation composition (biotic) variables (the two latter both being part of the environmental filter) for the small-scale variation in species and trait composition. Our study habitat was a mature Scots pine forest with well-developed understorey vegetation, resulting in - to the human eye - homogeneous environmental conditions, where we sampled the springtails using a spatially explicit sampling design. We sampled environmental conditions on the same spatial scale to enable variance partitioning of environmental and spatial variables. We expected the environmental variables to show little variation and thereby to have low influence on local community composition, aiming at detecting the importance of other factors shaping communities when environmental filtering is not strong. On the spatial scale of our study, individual samples were considered as local communities (i.e. a set of taxa interacting within a habitat) and the turnover is the variation between local communities, while the total sampled area is considered as a metacommunity composed of patches grading into each other.

For the trait-based approach we had access to trait information on all sampled species from a database consisting of over 350 species (M.P. Berg, unpublished data). Trait-based studies have proven useful to understand variation in community composition of springtails, for example as environmental conditions change (Krab et al., 2010; Makkonen et al., 2011; Bokhorst et al., 2012; Malmström, 2012; Martins da Silva et al., 2012; Salmon et al., 2014).

Because of the low horizontal heterogeneity of the pine forest habitat, biotic interactions (or dispersal limitation) were expected to play a larger role than environmental variation in explaining

variation in local community composition at this scale. We therefore hypothesized that (1) spatial variables would explain more of the variation in both species and trait composition than environmental (abiotic and vegetation) variables. We also expected that (2) local communities would consist of species more dissimilar to each other in traits than expected by chance due to limiting similarity mechanisms, and that (3) trait turnover between local communities would be smaller than expected by chance.

2. Methods

2.1. Study area

The study area was situated within a 160 year old Scots pine (*Pinus sylvestris* L.) forest in Jädraås, central Sweden (60°49′ N, 16°30' E). The forest has been used for forest management experiments since 1974, but the area selected for this study has been set aside as a control area, not receiving any treatments (i.e. thinning or clear-cutting) and has never been fertilized (T. Persson, personal communication). More details on the study area, soil properties and soil fauna can be found in Persson et al. (1980).

The area has a flat topography formed by glacifluvial sand. The understorey vegetation covered 90–100% of the ground, with a small-scale patchy distribution of bryophytes, mainly the red-stemmed feather moss (*Pleurozium schreberi* (Brid.) Mitt.), reindeer lichens (mainly *Cladonia rangiferina* (L.) Nyl.) and two dwarf-shrubs; common heather (*Calluna vulgaris* (L.) Hull) and cowberry (*Vaccinium vitis-idaea* L.).

2.2. Sampling design

We selected an area within the field site that was as homogenous in environmental conditions to the human eye as possible and that had no discernible topography. The sampling area (5 m × 20 m) was divided into a grid system of 100 squares, each 1 m^2 (Fig. S1). To ensure that enough short distances between samples were included for detecting patterns in species composition on less than a meter-scale, 25 of the 1 m × 1 m squares were randomly selected (stratified randomization to ensure that all parts along the 20 m side were covered) to include paired samples (10 cm × 10 cm) adjacent to each other. The location of the samples within each square was randomly selected based on 100 0.1 m × 0.1 m sub-squares. In addition, 50 squares were randomly (stratified) assigned one sample and in the remaining 25 squares no samples were taken. This design gave 100 samples, covering most parts of the sampled area (Fig. S1).

To avoid any stem- or canopy living species to end up in our samples, the distance to the closest tree from each sample was always larger than 20 cm from the closest corner of the sampling square to the beginning of the stem bark.

2.3. Collembola sampling

The sampling took place in October 2010. We marked the sampling grid with thin sticks and used a soil corer (10 cm × 10 cm metal square, 10 cm height) for sampling of the soil fauna, pushing it by hand into the litter layer (average height, 4 cm). The litter layer was immediately placed in plastic bags by hand. Thereafter, the underlying humus layer was sampled with an auger (6 cm diameter, ~10 cm height) pushed down until it reached the mineral soil (on average 5 cm), and also transferred into a plastic bag. All handling of samples was done quickly to avoid individuals escaping. Litter and humus samples were stored cool (~10 °C) until brought to the laboratory (the same or the next day) and then stored at 4 °C for extraction within three weeks.

We extracted soil fauna from the litter and humus layer separately. The litter was spread evenly on 20 cm × 20 cm nets (5 mm mesh size) while the humus layer was cut into 1 cm pieces and placed upside down on 3 mm mesh and placed in Tullgren funnels for 3 (humus) or 4 (litter) days. The samples were collected and stored in 70% ethanol. After extraction the litter and humus were stored cool (4 °C) in sealed plastic bags for chemical analyses.

Collembola species were identified to the species level, using identification keys by Fjellberg (1998, 2007), and counted.

2.4. Environmental and vegetation composition data

Understorey vegetation can affect soil communities, directly by giving shelter and affecting microclimatic conditions or resources, or indirectly through the amount of root exudation or litter production (Bardgett et al., 2005a). When the soil corer was placed at the sample point all plant and lichen species within the sample were identified (10 × 10 cm). This was later used as data on presence/absence (p/a) of lichens and bryophytes in each sample and, for dwarf-shrubs, as p/a of the two species *C. vulgaris* and *V. vitis-idaea*. At this time we also noted the dominant understorey species and the total vegetation cover (%) in the 10 cm × 10 cm squares.

Before extraction of the humus layer (see method, Section 2.3.) the depth of the litter (including vegetation) layer was measured with a line gauge, to nearest cm, on two opposing sides of the extraction point. This measure was averaged per sample. Before the soil fauna was extracted we removed the mineral soil from the samples and measured the humus depth (to the nearest cm).

After fauna extraction, the humus layer was homogenised by hand and used for soil chemical analyses. Loss-on-ignition of litter and humus was determined at 600 °C for 24 h, giving the percentage of organic matter in the soil by dividing the weight loss with weight of dry matter. The remaining homogenised humus was used for pH measurements.

2.5. Collembolan trait data

To examine the spatial variation in Collembola abundance and distribution of species across the plot we used traits that have previously been found to explain shifts in Collembola composition across time, space and environmental gradients (Krab et al., 2010; Makkonen et al., 2011; Bokhorst et al., 2012; Martins da Silva et al., 2012; Van Dooremalen et al., 2013; Widenfalk et al., 2015). The traits selected were *body length*, *antenna to body length ratio*, *life form*, *moisture preference* and *macro-habitat width* (see Table 1 for ecological significance). Trait values (Table S1) were obtained from a large Collembola trait database (M.P. Berg, unpublished data), mainly based on literature sources. Other possibly important traits, such as *feeding guild*, *fecundity* and *pH-tolerance* were not available for most species and therefore not possible to include in the study. We did not measure any traits, and therefore it was only possible to analyse the between, not within, species variation of trait values.

Habitat width, defined as the number of macro-habitat types where a species is commonly found based on literature data, has been shown to be important for explaining small-scale community composition in Collembola (Widenfalk et al., 2015) but is not a standardly used trait. Species that occur in a large number of habitats might be more tolerant against fluctuations in environmental conditions than species that are more specialized and found in a limited number of habitats. We listed all habitat types (14 macro-habitats in total based on Harding and Sutton (1985), i.e. cave, dune, alpine habitat, bog, marsh, seashore, peat/moor, heath, urban, waste ground, farmland, grassland/meadow, deciduous woodland, coniferous woodland) in which the encountered species have been found. We summed the number of habitat types per

Table 1
Definition of traits used in the study and the range of values (unscaled) for the species observed in the sampled area.

Trait	Definition	Ecological significance	Range of values or Categories
Body length	Maximum length from head to tip of abdomen (mm)	Connected to dispersal ability, life form, ecophysiology[a,b]	0.4–4.5 mm
Antenna to body ratio	Antennal length divided by body length	Assumed to be linked to sensory ability and active dispersal[c]	0.09–1.25
Life form	Trait complex composed of: number of ommatidia, length of body, and intensity of colouration[d]	Proxy for vertical stratification, ecophysiology and dispersal ability[b]	Epigaeic (0) Hemiedaphic (0.5) Euedaphic (1)
Moisture preference	Level of soil moisture content the species is mostly associated with[e]	Ability to tolerate high or low soil moisture content[f]	Xerophile (0) Xero-mesophile (0.25) Mesophile (0.5) Meso-hygrophile (0.75) Hygrophile (1)
Habitat width	Number of macro-habitat types in which the species has been found (see text for categories)	Tolerance to different environmental conditions, identifies generalists and specialists	1–7

[a] Berg et al. (1998).
[b] Ponge et al. (2006).
[c] Martins da Silva et al. (2012).
[d] Gisin (1943).
[e] Kuznetsova (2003).
[f] Makkonen et al. (2011).

species. This resulted in a maximum number of habitats for a species of seven, giving seven categories (1–7) of habitat width. Species stated in the literature to be found in "many habitats" were placed in the highest category (7).

2.6. Statistics

Abiotic environmental variables were only moderately correlated to each other and all were kept in further analyses (Pearson correlation coefficients $r < 0.5$, Table S2). Understorey vegetation data were included as presence/absence of the two dwarf-shrub species separately, of bryophytes and of lichens and as the species richness of the understorey vegetation observed in each sample.

Abundance data of each species were pooled for each sample of the separated litter and humus layer, after correction for the difference in sample area size between the two layers. This could result in undersampling of rare species in the humus compared to litter layer and an underestimation of diversity and species turnover between samples in the H-layer. We examined this by performing analyses of each layer separately and comparing this with the result from combining the layers. Furthermore, since the trait analyses are based on abundance weighted data (CWM), this effect should be negligible in the trait case.

To be able to combine traits with different units of expression in multi-trait analyses we scaled the values of each trait between 0 and 1 (before calculation of RaoQ and CWM, see Section 2.6.2 and 2.6.3):

$$V_{scaled} = (V - V_{\min})/(V_{\max} - V_{\min})$$

Pearson correlation tests between all traits showed that the measures of *life form*, *body length* and *antenna to body length ratio* were all positively correlated and *habitat width* was negatively correlated with *antenna to body length ratio* (Table S3). We decided to keep all traits for further analyses, as the levels of correlation were relatively low (r-values < 0.54, Table S3) and we believe that important information would be lost by eliminating some of the traits.

Spatial autocorrelation of Collembola total abundance of selected Moran's eigenvector maps (MEM) variables (Section 2.6.1) were tested with Moran's I tests (distance class 1 m, $p < 0.05$) and correlograms constructed using 'correlog' in R package pgirmess (Giraudoux, 2015).

2.6.1. Spatial variables – MEM analyses

The spatial configuration of samples was described by distance based Moran's eigenvector maps (dbMEM), a method based on computing the principal coordinates of a matrix of geographic neighbours (after Borcard et al., 2011), using 'spantree' in the R package vegan (Oksanen et al., 2015) and the package PCNM (Legendre et al., 2012). MEM analyses are considered robust and suitable for discriminating between spatial and environmental effects on community composition (Griffith and Peres-Neto, 2006). Each dbMEM-variable represents a spatial pattern at a given scale, from single maxima or minima within the study area to very small-scale variation with many maxima and minima (Fig. 1 gives some examples). We included MEM-variables describing significant spatial autocorrelation (only positive eigenvalues, see Dray et al. (2006)) and used forward selection ('forward.sel' function in the R package packfor, 999 permutations) to determine the variables to be included in the final models before analyses (Section 2.6.3 and 2.6.4) were performed. To be able to compare the effect of the different components (spatial, abiotic and vegetation) we included the same number of variables from each component (Cottenie, 2005). This meant that only the first five spatial variables from the forward selection were included in the final models.

2.6.2. Partitioning of species and trait diversity

To examine if there was higher species turnover than trait turnover between the samples we performed additive partitioning of species and trait diversity measures, as suggested by de Bello et al. (2009, 2010). The partitioning was done to assess the proportion of *within local community (alpha)* diversity and *among local communities (beta* = turnover) diversity, to *total regional community (gamma)* diversity. We used both species richness and the Simpson diversity index (hereafter referred to as Simpson) to describe species diversity. Simpson (when expressed as 1-D) is easily comparable with Rao's quadratic entropy (hereafter referred to as Rao) describing the community functional diversity (de Bello et al., 2009). If all species have exactly the same trait values Rao's quadratic entropy equals the Simpson diversity index (Botta-Dukat, 2005). For each of the five traits considered we calculated the Rao index at each sampling point (local community, α-Rao) using

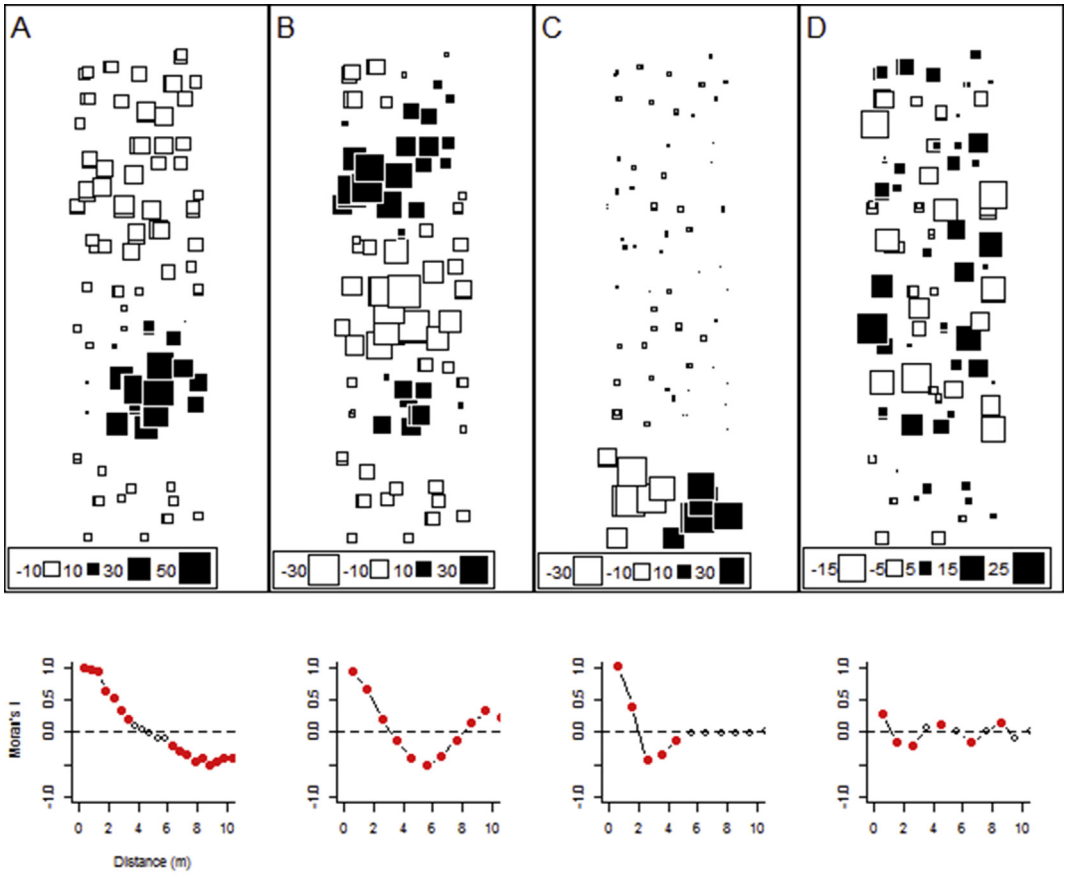

Fig. 1. Examples of Moran's eigenvector map (MEM) variables describing spatial patterns and included in the models. Variables A, MEM1 and B, MEM3 describe large scale spatial autocorrelation. Variable C, MEM9, represent a specific pattern in one corner of the sampling area (correlated with soil pH) and D, MEM23, is describing small scale spatial autocorrelation. Each square represents one sample (local community), values in the legends are the MEM eigenfunctions (principal coordinates of the truncated distance matrix), showing a gradient from one extreme to the other. Beneath each map the corresponding correlogram is shown, to illustrate the spatial scales of autocorrelation each variable represent. Filled circles indicate significant autocorrelation at that distance ($P < 0.05$) and Moran's I value gives the strength and directions of the correlation.

species abundance data, the abundance weighted Rao index of the whole sampled area (γ-Rao) and the turnover between local communities (β-Rao) by the additive approach of de Bello et al. (2010). By summing the dissimilarities of all traits, a multi-trait-Rao describing the functional diversity of the community (Botta-Dukat, 2005) can also be calculated and partitioned in the same manner into alpha, beta and gamma components. We used the dbFD function in the FD package (Laliberté and Shipley, 2011) to calculate the Simpson and Rao indices. To ensure independent beta and alpha values we used the equivalent number of alpha-, beta- and gamma diversity according to Jost (2007).

2.6.3. Trait underdispersion or overdispersion

To test if local communities had species with more similar (underdispersed) or less similar (overdispersed) traits than expected, we compared observed values of functional diversity (Rao) with null models of expected values. This was done by randomising species abundances within local communities, i.e. using the full set of species found in the study (the whole community) as the species pool, keeping the abundance distribution of species within each local community as observed but randomising the trait values assigned to each species (de Bello et al., 2009; Mason et al., 2012). If the observed α-Rao value is significantly ($P < 0.05$) lower than expected it is interpreted as trait underdispersion, i.e. that trait values are more similar than expected by chance, while a significantly higher value represents trait overdispersion. An observed β-Rao value lower than expected indicates a low turnover of traits (de Bello et al., 2009). α-Rao and β-Rao values for both observed values and null models were calculated as described in Section 2.6.2., for each of the five traits separately and for the multi-trait-Rao. We tested whether observed values differed from null models using one-sided permutation tests from the ade4 package in R (Dray and Dufour, 2007) with the function "as.randtest" and 999 permutations (0.05 significance level). If we find overdispersion in community composition horizontally, this could be due to vertical segregation of species so that some traits are predominantly found in the upper and others in the lower organic layers (Bokhorst et al., 2012). If so, significant overdispersion would not be found if we examine the layers separately. We checked this by performing the analyses for each of the litter and humus layers separately and comparing this to the pooled layers analysis.

2.6.4. The relationships between spatial, abiotic and vegetation variables and Collembola trait or species composition

To examine if Collembola species and trait composition can be explained by spatial, abiotic and biotic (vegetation) variables we used multivariate statistics. To separate the contribution of each component (spatial, abiotic and vegetation), we then performed variance partitioning of the three major explanatory components, but not separating the effect of the single explanatory variables that constitutes the three components. This enables us to disentangle the pure effects of each component, as well as show how much of

the variation that are explained by joint contribution by two or all three components and where it is not possible to separate their influence (Borcard et al., 1992).We calculated the community weighted mean of trait values (hereafter referred to as CWM) for each of the five traits using the method of Garnier et al. (2004), weighing species trait values in each sample by the relative abundance of the species. For analyses of species composition, species abundances were Hellinger-transformed, as the data included many zeros and we wanted to avoid to overemphasise rare species (Legendre and Gallagher, 2001).

Initial detrended correspondence analyses (DCA) of the species and CWM composition, respectively, showed a quite short gradient length (species composition: 1.740, traits CWM: 0.364) indicating only a weak unimodality in the data (ter Braak and Smilauer, 2002) and therefore we thereafter used linear model redundance analyses (RDA). RDA of the two datasets (species abundances and CWM trait composition) was performed using the function 'rda' in the R package vegan (Oksanen et al., 2015). Redundancy analysis of CWM is considered a suitable method to examine trait-environment relationships at the community level (Kleyer et al., 2012). The selected abiotic, vegetation and spatial variables were each tested separately and in combination, by multiple simple and partial RDAs. The proportion of the total variation explained by each component (group of variables) could be calculated using the sum of all canonical eigenvalues (Borcard et al., 1992), with function 'varpart' in vegan. To evaluate the performance of the different models, permutation tests (999 permutations, pseudo-*F* statistics) were performed on all separate models using 'anova.cca' from the R package vegan (Oksanen et al., 2015).

2.6.5. Variables related to the local community weighted mean of traits

To test if spatial, abiotic or vegetation variables best predicted the CWM of each trait, we performed multiple linear regressions with CWM as response variable and variables representing all three components as explanatory variables. Variables were centred before further analyses to be able to compare all the regressions (Schielzeth, 2010). Explanatory variables consisting of proportion-data (vegetation cover and organic content of soil) were arcsine(sqrt)-transformed.

Five variables from each group of explanatory variables were used in the total models (see section 2.6). Regressions using spatial, abiotic or vegetation variables alone were also conducted. Based on visual inspection, the residuals from the final regressions had close to normal distribution. The amount of variability explained by each group of predictor variables was assessed based on Sum of Squares decomposition, and compared with the residuals from each regression (Legendre and Legendre, 1998).

All analyses were performed in R version 3.2.0 (R-Core-Team, 2015).

3. Results

In total, we collected 23 426 Collembola of which 22 481 individuals were identified into 29 species and used in further analyses (leaving out unidentifiable juveniles and destroyed specimens). *Willemia anophthalma* dominated most samples (Table S4). Inspection of Coleman rarefaction curves showed that the study area was thoroughly sampled (Fig. S2). After approximately 35 samples the species accumulation curve levelled off towards an asymptote, where more than 90% of the final species richness was found. In total 99 samples from the study site were analysed. Moran's tests showed that the total abundance of Collembola was spatially autocorrelated at distances of 0.5–1.5 m (Moran's I 0.55–0.23, $P < 0.01$, Fig. S3).

Several spatial MEM-variables were included (and contributed significantly) in the analyses. The only one included (after forward selection) in all analyses was MEM9 (Fig. 1C). This variable represents a positive spatial correlation at 0.5–1.5 m (Moran's I 0.97–1, $P < 0.001$, Fig. S4), with two areas at one side of the sampled area very dissimilar to each other, and the rest of the samples having average values. MEM9 was also related to soil pH ($r = 0.59$) and to lower degree to proportion of organic material in humus and presence of *V. vitis-idaea* (Table S5). Other MEM-variables included in one or more analyses were related to either humus thickness, litter thickness, pH, organic material or presence of one of the vegetation categories (Table S5, Fig. 1).

3.1. Turnover in Collembolan trait and species composition

For all trait diversity measures, both averaged over all five traits (multi-trait-Rao) and for each individual trait, the local α-diversity accounted for almost all of the γ-diversity within the study area, with little or no turnover (β-diversity) of traits (Table 2). The turnover of species between samples was higher, contributing to 59% of the γ-SR and 34% of the Simpson γ-diversity (Table 2, similar result for the separate layers Tables S7 & S8). This shows that a few rare species contribute to a large part of the species richness turnover, and that the species turnover is not resulting in a turnover in trait diversity.

3.2. Trait underdispersion versus overdispersion

Most traits were overdispersed, i.e. showed a higher α-diversity than expected from the null model (Table 2, for details see Table S6). The trait *habitat width* had a significantly higher α-diversity than expected, i.e. each sample included both species with wide and species with narrow habitat "niches", but the β-diversity was not different from that expected (Table 2). The same was true for *moisture preference,* i.e. samples included both species preferring moist and those preferring dry conditions. For the traits *antenna to body length ratio*, a measure of sensory ability, and *body length* there was evidence of both overdispersion and a smaller β-diversity than expected – indicating that the trait-composition was more uniform across the samples than the species composition. The only trait not showing overdispersion was *life form*, which instead showed a higher turnover (β-diversity) between samples than expected (Table 2). Some parts of the study area were inhabited by more surface-living species while other parts had more of species that are classified as soil-dwellers. Since there was no significant underdispersion in the *life form* trait, most samples still had a range

Table 2
Regional (γ) trait diversity of Collembola in a mature pine forest and the proportional contribution of alpha (α) and beta (β) components to regional diversity (calculated after additive partitioning). Diversity is measured by trait diversity (Rao index, after Jost correction), species richness (SR) and species diversity (Simpson index, 1/(1-D) after Jost correction).Trait diversity values deviating from the null-model are shown as higher than expected (>exp) or lower than expected (<exp) (one-tailed permutation tests with 999 perm, $P < 0.05$).

	γ-diversity	% α	Test	% β	Test
Multi-trait diversity (RaoQ)	1.25	98	>exp	2	NS
Single trait diversities (RaoQ)					
Body length	1.08	99	>exp	1	<exp
Antenna to body length ratio	1.05	100	>exp	0	<exp
Life form	1.27	97	NS	3	>exp
Moisture preference	1.17	99	>exp	1	NS
Macro-habitat width	1.47	97	>exp	3	NS
Species richness (SR)	29	41		59	
Species diversity (Simpson)	5.87	66		34	

of species with different life forms. Taking all the five traits together (the *multi-trait Rao*) we found evidence for trait overdispersion, with higher mean α-diversity value than expected from a random distribution (Table 2). This can be interpreted as indicating niche separation, i.e. co-occurring species tend to have more different trait values than expected by chance.

3.3. Effect of environmental variables and spatial location on trait composition

The spatial variables and spatially structured abiotic variables contributed to most of the explained variation in Collembola trait composition, with pure abiotic and biotic variables explaining an additional few percentages (Fig. 2A). The same pattern was shown for species composition, although in this case the spatially structured abiotic fraction was much smaller than for trait composition, and the part explained by the pure spatial fraction contributed to >51% of the overall explained variation (Fig. 2B). When including each group of variables alone (i.e. only spatial, abiotic or biotic), all three components significantly explained some variation in species and CWM trait composition (Table 3). However, the pure biotic (vegetation) component did not in itself explain any variation in species or trait composition, when using the other two groups as co-variables (Table 3). Both spatial and abiotic variables still explained some variation when using the others as co-variables. The scale of spatial autocorrelation of the models was the same as for the total abundance of Collembola (Fig S3); the first RDA-axis of both species composition and CWM composition was positively autocorrelated at 1–2 m.

The single abiotic variable contributing most to the explained variation was soil pH, it explained 7.7% of the species and 21.7% of the trait variation. Among the single biotic variables, the presence of lichens explained 6.9% of the trait composition and the presence of *V. vitis-idaea* explained an additional 7.0% (similar numbers for species composition).

3.4. Effect of spatial and environment variables on the community weighted mean trait values

For all single traits the variation in CWM was explained by the spatial component to a higher degree than by abiotic and biotic environmental components, especially when considering pure effects (Table 4). This was despite of the fact that we selected fewer spatial variables than the forward selection suggested and thereby decreased the potential explanatory power of this component (group of variables). Pure space (i.e. after accounting for the variation explained also by abiotic and biotic variables) contributed to between 27 and 75% of the total amount of explained variation, and most of the remaining explained variation could be connected to spatially structured abiotic (or to a lesser degree biotic) variation. The spatial and environmental components could together predict 40–50% of the variation in CWM *habitat width* and CWM *life form*, but only 27% of the CWM *sensory ability* (adj R^2-values 0.27–0.50 $P < 0.001$, Table 4). pH contributed to the total model for the traits CWM *body length* and *life form*, i.e. when including all three explanatory variable components (spatial, abiotic and vegetation) pH was still significant in the analyses of these two traits (Table 5). The thickness of the humus layer contributed to the model of trait CWM *moisture preference*, while presence of *V. vitis-idea* contributed to explaining CWM *habitat width* and presence of *C. vulgaris* to CWM *body length* (Table 5).

4. Discussion

We selected a study area with a low horizontal heterogeneity in environmental variables because we wanted to examine the small-scale spatial patterns in local Collembola communities when the influence of environmental filtering was expected to be small. The important structuring forces are then assumed to be mainly biological interactions, especially competition, and small scale dispersal limitation (Hairston et al., 1960; Leibold et al., 2004). We found that the spatial factors explained most of the variation in species composition, much of the variation in trait composition, and also much or most of the variation in community weighted means (CWM) of all traits, supporting this prediction and our first hypothesis. Local communities (i.e. within each sample) showed overdispersion in all traits except *life form*, in agreement with our second hypothesis. This result suggests that within each local community there is a larger diversity in habitat specialisation, moisture specialisation, body length and sensory ability of the coexisting species than expected by chance, which can be explained by mechanisms related to limiting similarity, such as competition,

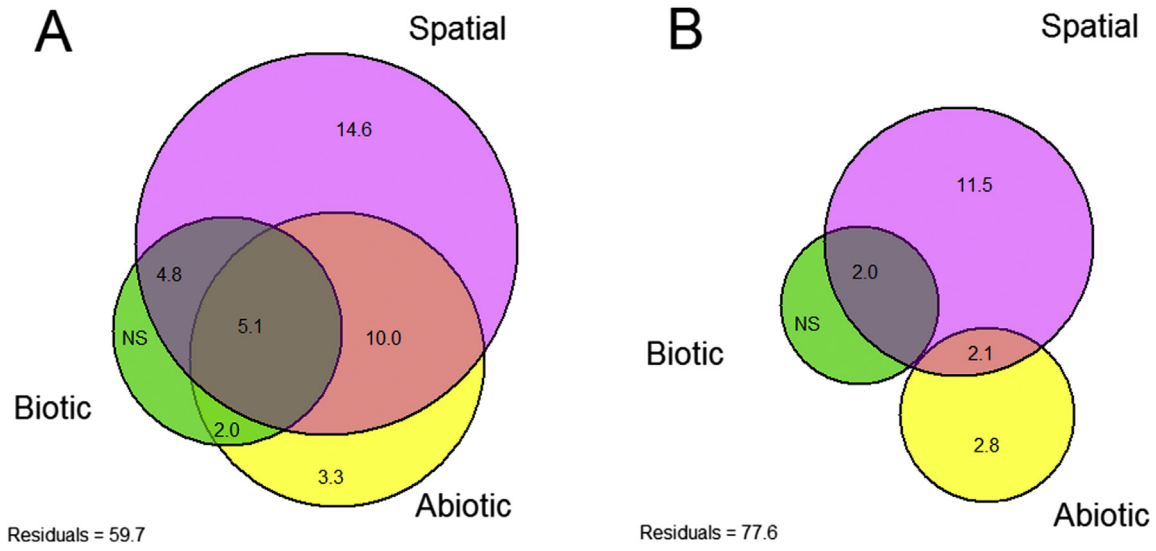

Fig. 2. Proportions of explained variation (%) by the three components (spatial MEM variables, abiotic variables and biotic vegetation variables) and their joint effects, for variation in Collembola A, CWM trait and B, species composition. Colours are used to make distinctions between the three components and show the overlaps between different fractions.

Table 3
Spatial variables explain the largest part of total explained variation in Collembola trait composition in a mature pine forest, based on variation partitioning including also abiotic and biotic variables as explanatory components. Shown are results from all separate RDA-analyses with CWM traits as response matrix.

	Explanatory variables	Co-variables	df	Adjusted R-sqr	Variance (inertia)	F-value	P-value
Total explained variation	S + B + A	–	15	0.40	0.0076	5.41	0.001
Pure Spatial[a]	S	B + A	5	0.15	0.0025	5.30	0.001
Total Spatial	S	–	5	0.35	0.0058	11.33	0.001
Pure Abiotic	A	B + S	5	0.03	0.0009	1.98	0.029
Total Abiotic	A	–	5	0.20	0.0038	6.04	0.001
Pure Biotic	B	S + A	5	0.004	0.0005	1.12	0.35
Total Biotic	B	–	5	0.12	0.0026	3.78	0.004
Spatial and Abiotic	S + A	–	10	0.40	0.0071	7.50	0.001
Abiotic and Biotic	A + B	–	10	0.27	0.0051	4.39	0.001
Biotic and Spatial	B + S	–	10	0.37	0.0067	6.74	0.001

S = Spatial (MEM) variables, B = Biotic (vegetation) variables, A = Abiotic variables.
p-values are based on permutation tests of all canonical axes, under reduced model, with *pseudo-F* test statistics. Total variation (SS) = 1.50, Variance/Inertia = 0.0151, Spatial variables included were (in order of inclusion): MEM9, MEM6, MEM1, MEM3 and MEM23, for Abiotic and Biotic variables included see Section 2.6.
[a] Pure effects are the explained variation by one component, when removing the variation also explained by either of the other two components. All other fractions given are the proportion of variation explained when including one, two or all three components, respectively.

Table 4
Pure spatial variables, or spatially structured abiotic variables, explain the largest part of total explained variation in all CWM trait values. The contribution of pure abiotic and biotic variables varies, but are consistently lower. Based on variation partitioning of each CWM trait from multiple linear regressions (values are adjusted R^2, significant fractions are written in bold, $^{*}P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$, *P*-values cannot be given for joint effects).

	Body length	Antenna/body length ratio	Life form	Moisture preference	Macro-habitat width	Df
Total explained variation (=adj R^2)	**0.358*****	**0.265*****	**0.499*****	**0.395*****	**0.411*****	**15**
Pure Spatial[*]	**0.126*****	**0.198*****	**0.136*****	**0.261*****	**0.211*****	5
Pure Abiotic	**0.045***	0.019	**0.070****	0.027	-0.015	5
Pure Biotic	**0.052***	-0.003	0.004	-0.032	0.028	5
Joint effect Spat*Abio	0.097	0.015	0.144	0.051	0.051	0
Joint effect Abio*Bio	-0.009	0.018	0.012	0.008	0.022	0
Joint effect Bio*Spat	0.013	0.019	0.048	0.032	0.054	0
Joint effect Spat*Abio*Bio	0.035	-0.002	0.084	0.048	0.062	0
Unexplained	0.642	0.735	0.501	0.605	0.589	

[*]Pure effects are the explained variation by one component, when removing the variation also explained by either of the other two components. Joint effects are when two components are either affecting each other or simply co-vary, so that their individual contribution on the response variable cannot be separated. Negative values (shown in grey shade) should be interpreted as no variation explained by that particular fraction.

but not to dispersal limitation.

There is thus some support for our hypothesis of no strong environmental filtering in these local communities. The variation partitioning showed a high pure effect of space but no strong pure effects of either biotic or abiotic variables for our Collembola community. None of the environmental variables, neither the abiotic nor the vegetation component, had a major impact on species composition, as shown by the full models (Table 5). The larger joint effect (spatially structured abiotic and biotic fractions) for trait composition could be caused by environmental filtering that cannot be disentangled from spatial effects. That is, the joint effect in a variation partitioning only shows that the effects of the two (or three) sets of factors cannot be separated statistically, and does not necessarily indicate any causal effects. Our study area was a mature pine forest with short environmental gradients and stable environmental conditions for the Collembola community. With a low variation in environmental conditions there is little potential for strong external factors eliminating or favouring certain species in any particular part of the studied area. Previous studies have often found that Collembola community composition is better explained by environmental than spatial variables. This was the case when several different habitats were included in regional scale studies (i.e., usually > 1 km) (Martins da Silva et al., 2012; Ponge and Salmon, 2013), or at the local scale of < 30 m in a habitat subjected to spatially structured disturbances (Widenfalk et al., 2015). The Collembola community in our study showed spatial autocorrelation within 1 m, indicating that the community is in fact structured at this small spatial scale. However, the lack of strong environmental filtering in our study suggests that the relative importance of environmental and spatial factors is related to the spatial scale and extent of a study and the length of environmental gradients within the study area, i.e. the environmental variation between samples. Increasing the length of any environmental gradient, regardless of spatial scale but more likely to occur when increasing the spatial distance, will probably result in an increase of the impact of environmental filtering. This can be seen as a higher probability of finding underdispersion in communities when conducting studies at relatively large spatial scales (Gotzenberger et al., 2012). A study of mite communities at the same spatial scale as our study found that the spatial component explained an even higher fraction of the variation than in our study (Gao et al., 2014), supporting this general interpretation.

Understorey vegetation composition explained even less of the variation in Collembola community composition than abiotic variables, despite the visually obvious small-scale patchiness of the vegetation composition of the site. Although vegetation could explain some of the variation in the Collembola community (when not considering the other groups of variables), this is more likely to reflect the fact that both vegetation and the Collembola community are structured by the same abiotic variables and/or at the same spatial scales. It has previously been found that during primary succession or harsh conditions plant species richness may determine the assembly of Collembola communities (Coulson et al., 2003; Ingimarsdottir et al., 2012) but that doesn't seem to be true in the later successional stages presently studied, with more stable environmental conditions. Additionally, fungal composition is

Table 5
Summary of multiple linear regressions of all CWM trait values with abiotic, biotic and spatial variables as predictors. Space is described by (forward) selected MEM-variables. For the included variables, their estimates and significance (bold) in each multiple regression is given. All models have $P < 0.001$, adjusted R^2-values are the 'total explained variation' in Table 4.

TRAIT	Explanatory variables[a]		
	Spatial	Abiotic	Biotic
Body length	**MEM9 (0.0008)***	**Soil pH (0.0398)***	Bryophytes (−0.0035)
	MEM7 (0.0008)**	Litter (0.0031)	Lichens (−0.0105)
	MEM1 (0.0003)	Humus (0.0015)	***Calluna* (−0.0250)***
	MEM12 (0.0005)	Organic mat. (0.0369)	*Vaccinium* (−0.0293)
	MEM2 (0.0003)	Cover (0.0132)	SR (0.0001)
Antenna/body length ratio	**MEM12 (0.0008)*****	Soil pH (0.0208)	Bryophytes (0.0024)
	MEM1 (0.0004)**	Litter (0.0005)	Lichens (−0.0075)
	MEM2 (0.0003)*	Humus (0.0032)	*Calluna* (−0.0104)
	MEM9 (0.0001)	Organic mat (−0.0139)	*Vaccinium*(−0.0113)
	MEM18 (−0.0007)*	Cover (0.0029)	SR (0.0017)
Life form	**MEM9 (−0.0022)****	**Soil pH (−0.1280)*****	Bryophytes (−0.0041)
	MEM1 (−0.0013)**	Litter (0.0029)	Lichens (0.0196)
	MEM7 (−0.0008)	Humus (−0.0035)	*Calluna* (−0.0309)
	MEM20 (−0.0021)*	Organic mat. (−0.0493)	*Vaccinium* (0.0266)
	MEM4 (−0.0004)	Cover (0.0118)	SR (0.0047)
Moisture preference	**MEM9 (−0.0017)****	Soil pH (−0.0256)	Bryophytes (−0.0056)
	MEM3 (−0.0015)***	Litter (0.0030)	Lichens (−0.0041)
	MEM6 (0.0008)*	**Humus (0.0089)***	*Calluna* (0.0014)
	MEM23 (0.016)*	Organic mat. (0.0126)	*Vaccinium* (0.0065)
	MEM2 (0.0007)*	Cover (0.0037)	SR (−0.0012)
Habitat width	**MEM9 (−0.0022)*****	Soil pH (−0.0121)	Bryophytes (0.0000)
	MEM6 (0.0011)**	Litter (0.0055)	Lichens (0.0028)
	MEM1 (−0.0007)*	Humus (−0.0001)	*Calluna* (−0.0111)
	MEM15 (−0.0001)*	Organic mat. (−0.0127)	***Vaccinium* (0.0531)***
	MEM22 (−0.0012)	Cover (0.0117)	SR (0.0102)

Spatial variables consist of MEM-variables with positive eigenvalues with low numbers representing relatively large scale patterns and MEM25 the smallest scale patterns detectable with this design, for more details see Section 2.6. Soil pH = pH in the humus and lower litter layer, Litter = thickness of litter layer, Humus = thickness of humus layer, Organic mat. = proportion organic material in humus and lower litter layer, Cover = proportion of ground area covered by vegetation/litter. All vegetation variables are measured as presence/absence; Bryophytes = mosses, Lichens = mainly *Cladina* sp., *Calluna* = *C. vulgaris*, *Vaccinium* = *V. vitis-idaea*, SR = species richness of ground vegetation. All variables included in the final regression models are shown, for MEM-variables the first five selected from forward selection were included.

[a] After each variable the estimate value in the final model is given within brackets, significance level is shown by number of *. *P < 0.05, **P < 0.01, ***P < 0.001.

likely to have a stronger impact on the Collembola community (Klironomos and Kendrick, 1995), but such information is lacking in our study.

There was almost no turnover in the analysed traits across the study plot, i.e., all local communities had the same set of functional traits. Trait turnover in the studied pine forest was lower than reported from similar studies of Collembola community composition at similarly small spatial scales (e.g. Widenfalk et al., 2015). Due to the lack of strong environmental gradients in our studied area most species in the regional pool are likely able to live in most patches and species interactions or stochastic events are the most likely causes for species to be missing from certain patches. This results in communities possessing more or less the same set of traits over the entire area. We show that in this seemingly very homogeneous habitat we also find a Collembola community that appears homogeneous. However, the species turnover between samples 0–30 m apart was higher than the trait turnover, a result that has been found for several other organism groups previously (see e.g. de Bello et al., 2009; Astor et al., 2014) as well as for Collembola (Widenfalk et al., 2015). The turnover in Simpson diversity was also lower than the turnover in species richness, indicating that the turnover in species was mainly due to rare species found in few samples and not to changes in dominating species.

Spatially structured communities, without a connection to strong environmental filters - in our case indicated by consistent trait overdispersion (Table 2) -, are usually interpreted as a result of biotic interactions or dispersal limitation (Leibold et al., 2004). Another possible explanation for strong spatial structure (considering the ecological characteristics of most Collembola) could be aggregated reproduction (e.g. Atkinson and Shorrocks, 1984). Combined with a low dispersal ability this could result in aggregation of species depending on exactly where in a suitable habitat they select to deposit their eggs. In our study the local communities (samples) showed overdispersion, i.e. species were more different from each other than expected by chance in certain traits (Table 2). Patterns of overdispersion indicate that competitive exclusion due to niche segregation is likely a major factor in structuring communities (HilleRisLambers et al., 2012). In contrast, dispersal limitation or aggregation would lead to underdispersion or more or less random trait distributions. In stable environments, such as the studied mature pine-forest floor, there is a higher chance for biotic interactions such as competition to influence species distributions (Menge and Sutherland, 1976). The local communities (samples) consisted of species with a higher diversity in *habitat width* than expected if the community had been assembled by random from the regional species pool, i.e. they included both specialist and generalist species. Having different strategies for habitat selection thus seems to enable species to co-exist (cf. Aunapuu and Oksanen, 2003).

Our results suggest that competition may be an important structuring process in Collembola and other soil fauna communities, as has been indicated in some recent studies (Caruso et al., 2013; Leinaas et al., 2015). Coexisting species showed divergent strategies in resource utilisation, implying that species competing for the same resource, e.g. food or pore size, exclude each other from certain areas. Previous studies examining feeding guilds and food preference of Collembola have shown that there could be larger differences among species than previously believed, explaining the coexistence of many species assumed to compete for the same resources (Jorgensen et al., 2003; Berg et al., 2004;

Chahartaghi et al., 2005).

Another explanation for overdispersion within samples could be vertical microhabitat selection, where species live in different layers of the soil profile. Short-scale environmental gradients in microclimate and resource quality down the soil profile have been shown to result in different Collembola communities with depth in the soil (see e.g. Faber and Joosse, 1993; Berg et al., 1998; Berg and Bengtsson, 2007; Krab et al., 2010). This could act as an environmental filter if analysed at the micro-habitat scale (with species with certain traits selecting one vertical micro-habitat) but is misinterpreted as a biotic filter when not taking this into consideration. That we find overdispersion in *sensory ability* may be linked to vertical stratification, as species living in deeper soil layers tend to have reduced antenna length. To examine if this is driving the patterns of overdispersion, we analysed the litter-dwelling and humus-dwelling communities separately. In the humus layer we found overdispersion in two traits only – *sensory ability* and *habitat width* – and no or lower than expected beta diversity (Table S7). In the litter layer samples, all traits except *life form* showed overdispersion (Table S8) consistent with the results for combining the two layers, indicating strong evidence for biotic interactions. The litter communities also had a lower turnover (β-diversity) than expected for three of the traits – *body length, sensory ability* and *moisture preference* – but higher than expected for trait CWM of *habitat width* and *life form*. Although there were some differences between the trait composition of the upper and lower soil layers, these results suggest that the observed overdispersion in Collembola community traits cannot be explained by species with different traits selecting different layers.

For the traits *antenna to body length ratio* (*sensory ability*) and *body length* we found a smaller turnover than expected from random assembly, but for *moisture preference* this could only be detected when analysing the litter layer separately. However, the very low turnover in species found in our study could make it hard to observe a significantly lower value of β-diversity than expected by chance. The trait *life form* contradicted our expectations and had a higher turnover than if communities had been randomly assembled. This could be linked to the pH-value of the patches, with deep-living species like *W. anophthalma* and *M. yosii* being more connected to acidic soils (pH ~ 3.5–4.5) (Hågvar, 1990), and a few of our samples with pH around 5.0 having more surface-living species. The variation in CWM *life form* was explained by both pH and spatial parameters, where the variable MEM9 (the spatial parameter correlated to pH) was one of the selected MEMs.

Overall our results suggest that the Collembola community in this mature pine forest is structured mainly by species interactions, such as competition, as species are more likely to coexist when having different strategies in resource utilisation. However, pH also seemed to have some influence on the community structure. The study also supports the old ideas of high redundancy in soil communities (Anderson, 1975; Takeda, 1987), i.e. that many species possess similar functional traits (characteristics) and that thereby the removal of single species may not change the functioning of the Collembolan community. Finally, our study shows the power of combining variation partitioning with analysis of community assembly to understand the factors structuring soil community composition.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.soilbio.2016.08.006.

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